HIPPOCRATEA VOLUBILIS (CELASTRACEAE) IN COTUI COPAL FROM THE DOMINICAN REPUBLIC

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ABSTRACT

Four fossil flowers of *Hippocratea volubilis* were found preserved in copal from ground deposits near Cotui, Dominican Republic. The specimens fall within the pattern of morphological variation of this widespread New World species. The time of deposition of the copal is uncertain, the estimates ranging from under 1000 ybp to Miocene. The younger age is supported by carbon-14 dating from 2 laboratories, whereas the older date is based on measurements from proton magnetic resonance spectroscopy. Assignment of these fossils to a modern species supports an age of less than 1000 years for the Cotui deposits.

RESUMEN

Cuatro flores fósiles de Hippocratea volubilis se encontraron conservadas en copal en depósitos cerca de Cotui, República Dominicana. Los especimenes coinciden en su patrón de variación morfológica de esta especie frecuente del Nuevo Mundo. El tiempo de deposición del copal es incierto, las estimaciones varían desde por debajo de 1000 ybp hasta el Mioceno. La edad más reciente esta soportada por datación mediante carbono-14 en 2 laboratorios, mientras que la edad más antigua está basada en medidas de espectroscopía de resonancia magnética de protones. La asignación de estos tres fósiles a una especie moderna soporta una edad de menos de 1000 años para los depósitos de Cotui.

INTRODUCTION

Fossilized resin in the Dominican Republic occurs in a number of small mines in the northern and eastern portion of the country. The fossil material from these mines consists of amber and has been dated at 15–20 mybp using foraminifera index fossils (Itturalde-Vinent & MacPhee 1996) and at 20–45 mybp with coccolith index fossils (Cepek in Schlee 1990). Some softer, clearer material from the vicinity of Cotui has also been collected; however, the age of this is uncertain, although it has generally been considered younger than the amber. It is often referred to as "copal" or semi-fossilized resin, which differs from amber in a number of physical properties. Copal occurs in various parts of the world, especially in South America and New Zealand (Poinar 1992). It can be considered "young amber," and under the right conditions it could mature into amber after millions of years.

The flowers described here are members of the genus *Hippocratea* (Celastraceae, Hippocrateoideae), as defined by Smith (1940, p. 357). Three of the flowers are illustrated; the fourth is darkly pigmented and unsuitable for study. All are bisexual and in the pistillate phase, with stamens recurved and style elongated (Matthews & Endress 2005). The conical disc enclosing the pistil is divided horizontally into 2 sections and is minutely papillate throughout. The petals are imbricate at the base and abaxially tomentulose, with villous-ciliate margins. Pubescence of the adaxial surface consists of villous trichomes in a transverse band below the apex, equivalent to the "transversely barbellate" condition described by Smith (1940, p. 360) for *H. volubilis*. The sepals are ovate, imbricate, and minutely papillate abaxially. Based on comparison with a series of herbarium specimens of *H. volubilis* respecting these and other floral features, we identify the fossils as conspecific with this taxon.

Published estimates of the age of Cotui copal have ranged from Miocene to as young as 1000 ybp or less. Our conclusion that the *Hippocratea* flowers are assignable to the extant species *H. volubilis* strongly supports the latter, younger age, which was obtained from carbon-14 dating in 2 laboratories ("Beta Analytic" in the United States and "Harz aus dem Tennengebirge" in Germany).

Hippocratea pollen is well represented in the fossil record (Muller 1981), but to our knowledge these are the first fossil flowers of the genus to be discovered.

MATERIALS AND METHODS

The specimens were collected from the upper 8 inches of soil at Zambrana Abajo near Los Ranchos in the vicinity of Cotui, a village located in a valley between the Cordillera Central and Cordillera Septentrional, Dominican Republic. The material is clear with a yellow tinge. Many samples are collected by children who follow the plows during the planting of maize (personal correspondence from the late Jake Brodzinsky, 20 September 1987).

The age of fossilized resin from Cotui is unclear. Because of its light color and fairly soft texture, it has been referred to as copal, a term used for semi-fossilized resin that possesses specific physical properties related to color, hardness, melting point, and solubility (Poinar 1992). Age estimates range from under 1000 years, based on radiocarbon dating (Schlee 1984, Poinar, unpublished results), to Miocene, based on proton magnetic resonance spectroscopy (Lambert et al. 2012). In support of the older age was the discovery, in the copal, of several new insect species now considered to be extinct (Popov 1987; De Andrade & Baroni Urbani 1999).

Comparing the maturity of fossilized resins with that of their enclosing bedrock can provide information on the maturity, relative age, and biostratinomy of amber and copal. Such a study was conducted on amber and Cotui copal from different mines in the Dominican Republic (Poinar & Mastalerz 2000). Maturity of the bedrock was determined by vitrinite reflection and that of the fossilized resin by FTIR (Fourier Transform Infrared Analysis). The study found that Cotui copal showed a lower degree of maturity than that of the matrix rock, indicating that it had been washed into the older bedrock fairly recently and probably represents deltaic deposits. Further analysis of Cotui copal revealed that the plant source of the resin was *Hymenaea courbaril* (Mastalerz & Poinar, unpublished observations), a tree species that still exists on Hispaniola.

DESCRIPTION

Hippocratea volubilis L. (Figs. 1–5). Fossil specimens examined: HISPANIOLA. Dominican Republic: vicinity of the town of Cotui, in a valley between Cordillera Central and Cordillera Septentrional, 2012, unknown amber collector (catalogue numbers Sd-9-105A, Sd-9-105B), and J. Brodzinsky s.n., 1987 (Sd-9-105C), deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.

Flowers bisexual, total length (pedicel apex to tip of style) 2.4 mm, calyx shallowly cupulate (Fig. 2), sepals 5, ovate, imbricate, 0.6–0.8 mm long, 0.8–0.9 mm wide, blunt-tipped, abaxially papillate, petals 5, spreading, lanceolate-elliptic, 2.1 mm long, 1.2 mm wide, 7–9-nerved, slightly overlapping at the base (Fig. 5), tip incurved, abaxial surface tomentulose with short, curved trichomes, adaxial surface with villous trichomes in a broad to narrow transverse band or arc slightly more than half-way distal from the base (Figs. 1, 4), sometimes papillate in a band proximal to the villous trichomes (Fig. 1), the central portion otherwise glabrous and distinctly veined downward to the base (Figs. 1, 4, 5), margins ciliate-villous (Figs. 1, 2), disc 1.3 mm high, 1.7 mm in diameter, pulvinate, conical, enclosing the ovary, 2-parted, enlarged below and above the mid-line (Figs. 1, long, 0.3 mm wide, strap-shaped, abaxially papillate near base (Fig. 1), anthers terminal, bilocular, ovoid, 0.4 mm long, puberulent.

DISCUSSION

For the purpose of comparison, we assumed that *Hippocratea volubilis*, which is widespread in Central and South America and the Caribbean region, is likely to be the extant species most closely related to the fossils.



Fig. 1. Flower A, apical view, showing bilobed form of the disc. Note villous-ciliate margin and involute tip of petals. Short arrow points to abaxial papillae on filament. Long arrow designates band of papillate trichomes on adaxial petal surface. Bar = 1 mm.

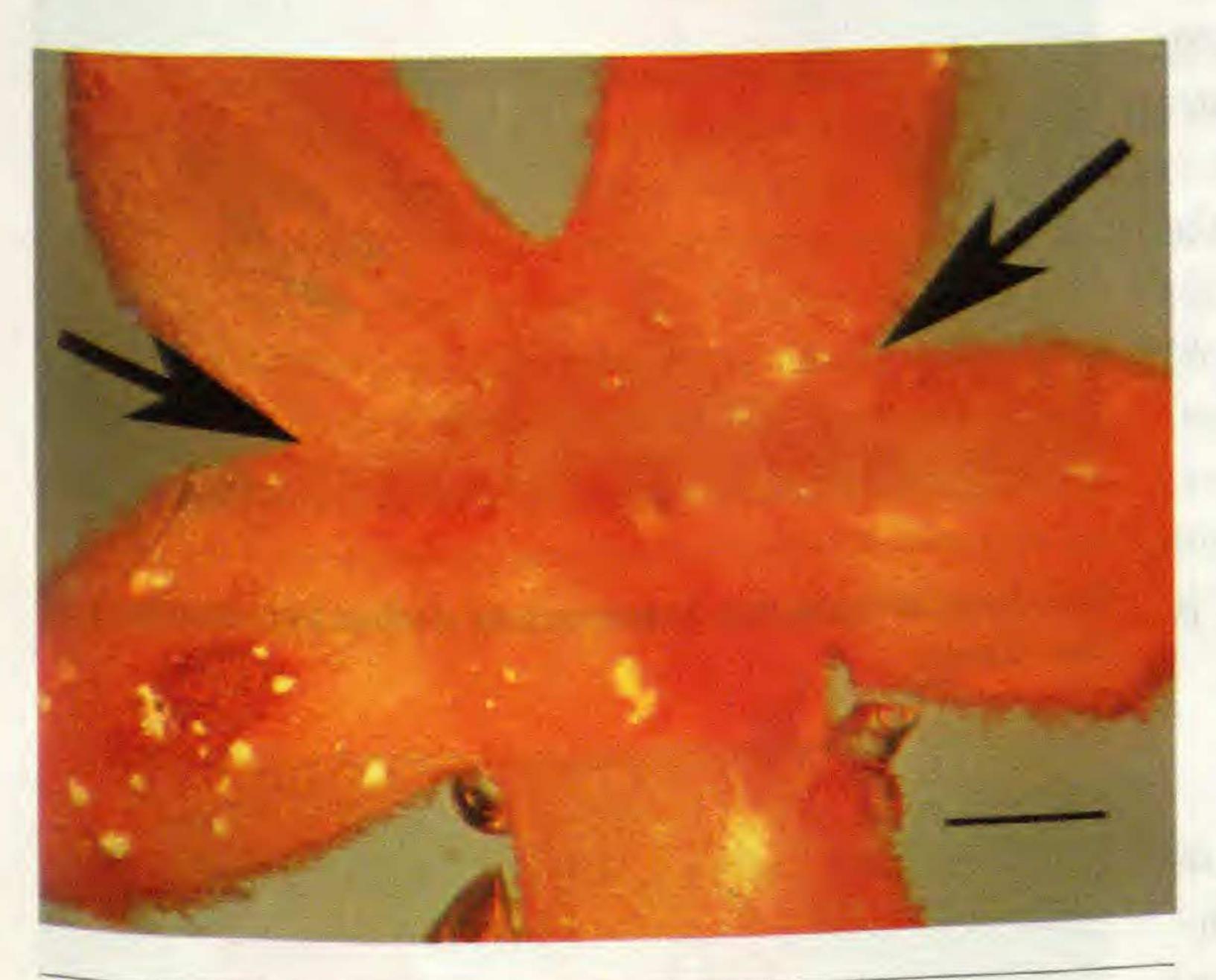


Fig. 2. Flower A in basal view, showing calyx and abaxial petal pubescence. Note villous-ciliate petal margins. Arrows point to 2 sepals alternating with petals. Bar = 0.6 mm.

The copal flowers are in the female stage of maturation, with reflexed stamens and elongated style, as illustrated by Matthews and Endress (2005, figs. 49, 50). The adaxial pubescence of the petals consists of a conspicuous band or arc of villous trichomes, which is essentially similar to the pubescence pattern in herbarium specimens of H. volubilis. Such trichomes were, in fact, cited by Smith (op. cit., p. 357) as a diagnostic trait of the genus. The petals of the flowers appear from photographs to be slightly connate, but careful microscopic study shows them to be basally imbricate. The floral disc is divided into upper and lower segments, thus differing from Smith's illustration of H. volubilis (op. cit., p. 357). However, similar 2-parted discs are often present in herbarium specimens of that species, including many from the Caribbean region. In A. & P. Liogier 30929, Puerto Rico (US2996525), for example, the upper and lower disc segments are sharply differentiated, with both parts being papillate, as in our fossils. In both C.V. Morton 7839, Honduras (US202361) and R.S. & E.S. Howard 9817, Dominican Republic (US2228804), on the other hand, the upper half of the disc is much more prominently papillate than the lower half. The upper section of the disc is sometimes reduced to a narrow papillate band below the anthers (e.g., D.K. Christopher et al. 69, NY s.n., Puerto Rico). A peculiarity of petal pubescence in both the modern and fossil flowers is that a zone of papillate trichomes may or may not be present proximal to the adaxial band of villous trichomes. This is illustrated in Fig. 1, although the microscopic nature of these papillae often makes them difficult to observe.

In the conservative taxonomic treatment by Smith (1940), Hippocratea was made monotypic, and over 40 existing specific and varietal names were synonymized under the single species H. volubilis. He limited this taxon to the tropics and subtropics of the New World, where its range extends north as far as the Everglades of Florida (Long & Lakela 1971). The pubescence of perianth, disc, androecium, and peduncle in the Cotui fossils, as described above, falls within the variation that we observed in available herbarium specimens of H. volubilis. With the exception of petal length and width, the sizes of floral parts in the fossils are within the ranges given for H. volubilis in Smith's species description (op. cit., p. 360). The petals are slightly shorter (2.1)

vs. 2.5–4 mm) and narrower (1.2 vs. 1.3–2.6 mm) than measurements cited by Smith for the extant species. There is no indication that these quantitative differences are due to the process of preservation.

The assignment of the flowers to an extant species favors the more recent of the two conflicting age estimates for Cotui copal, namely an age of 1000 years or less, commensurate with the results from carbon-14 dating.

Hippocratea and its allied genera, once recognized as the separate family Hippocrateaceae (Smith 1940; Loesener 1942; Long & Lakela 1971; and others), are now included in family Celastraceae as subfamily Hippocrateoideae (Simmons 2004, Matthews & Endress 2005, Stevens 2001 onwards). Molecular phylogenetic studies by Savolainen et al. (1997, 2000), Simmons et al. (2001a, 2001b), and others confirm this relationship. The subfamily has been shown to comprise a monophyletic group (Simmons et al. 2001b, Simmons 2004), but the tribe Hippocrateeae, to which the genus is assigned, is not monophyletic unless tribe Campylostemoneae is included (Simmons et al. 2001b).

The described specimens appear to be the first recorded sub-fossil flowers of the genus. They will be useful to future monographers, floristics workers, and paleontologists interested in the Caribbean region. As noted above, there are pollen records of *Hippocratea* from the Oligocene and lower Miocene (Muller 1981, p. 81).

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REFERENCES

DE Andrade, M.L. and C. Baroni Urbani. 1999. Diversity and adaptation in the ant genus Cephalotes, past and present. Stuttgarter Beitr. Naturk. Ser. B 271:1–889.

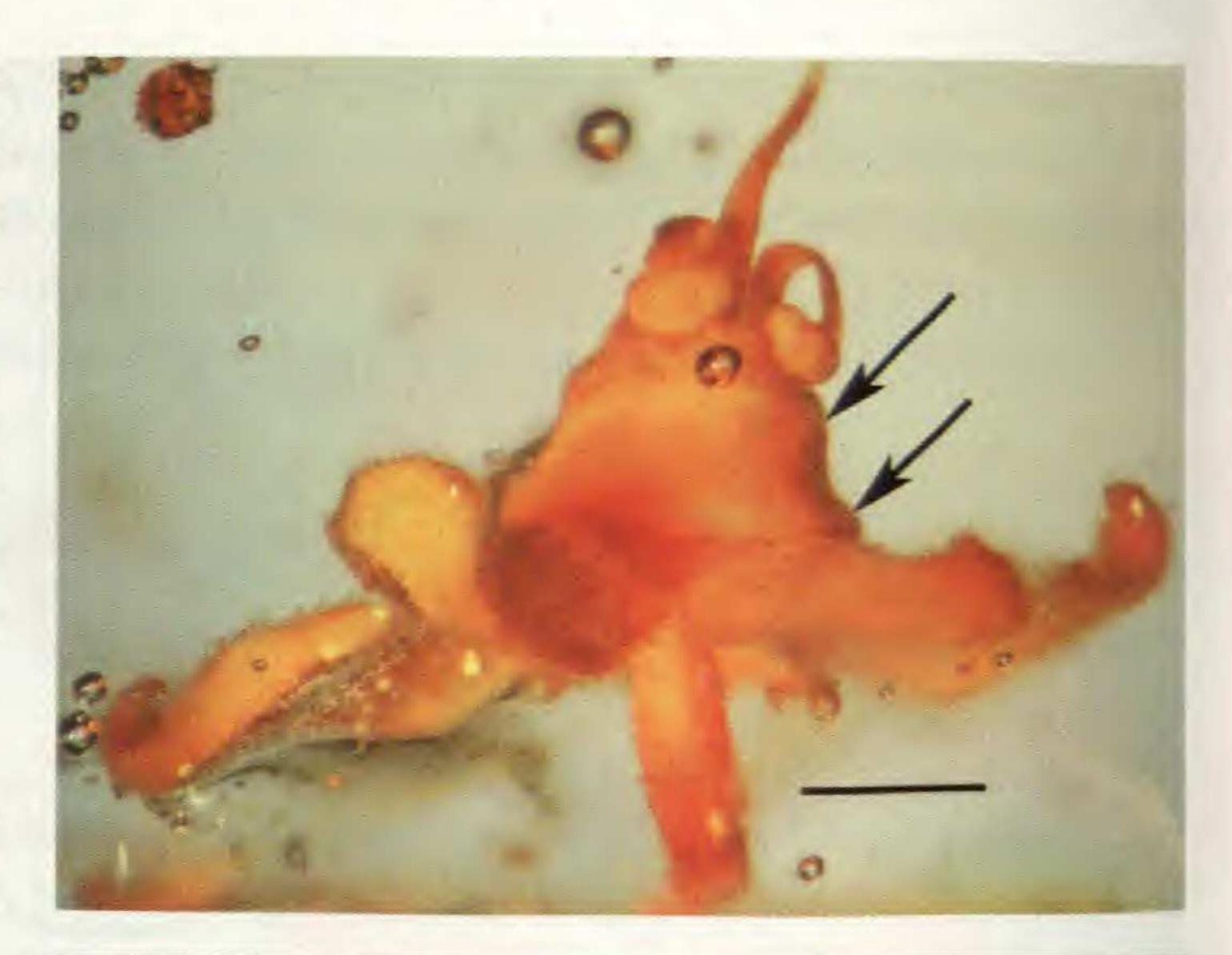


Fig. 3. Flower A in lateral view, showing reflexed stamens and bilobed form of the disc. Arrows point to 2 zones of enlargement of the disc. Bar = 0.8 mm.

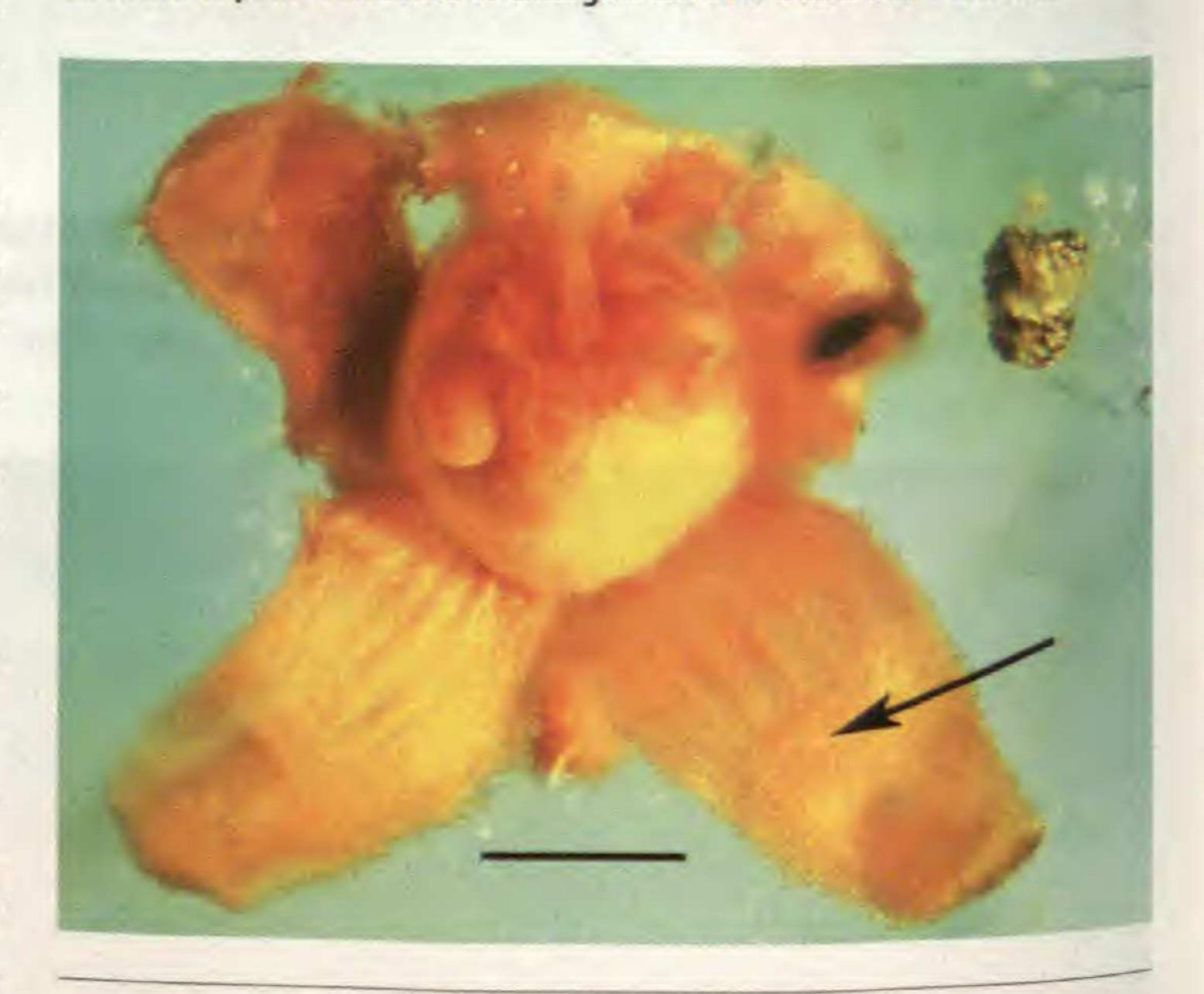


Fig. 4. Flower B in apical view. Arrow is on band of villous trichomes across petal. Bar = 0.8 mm.

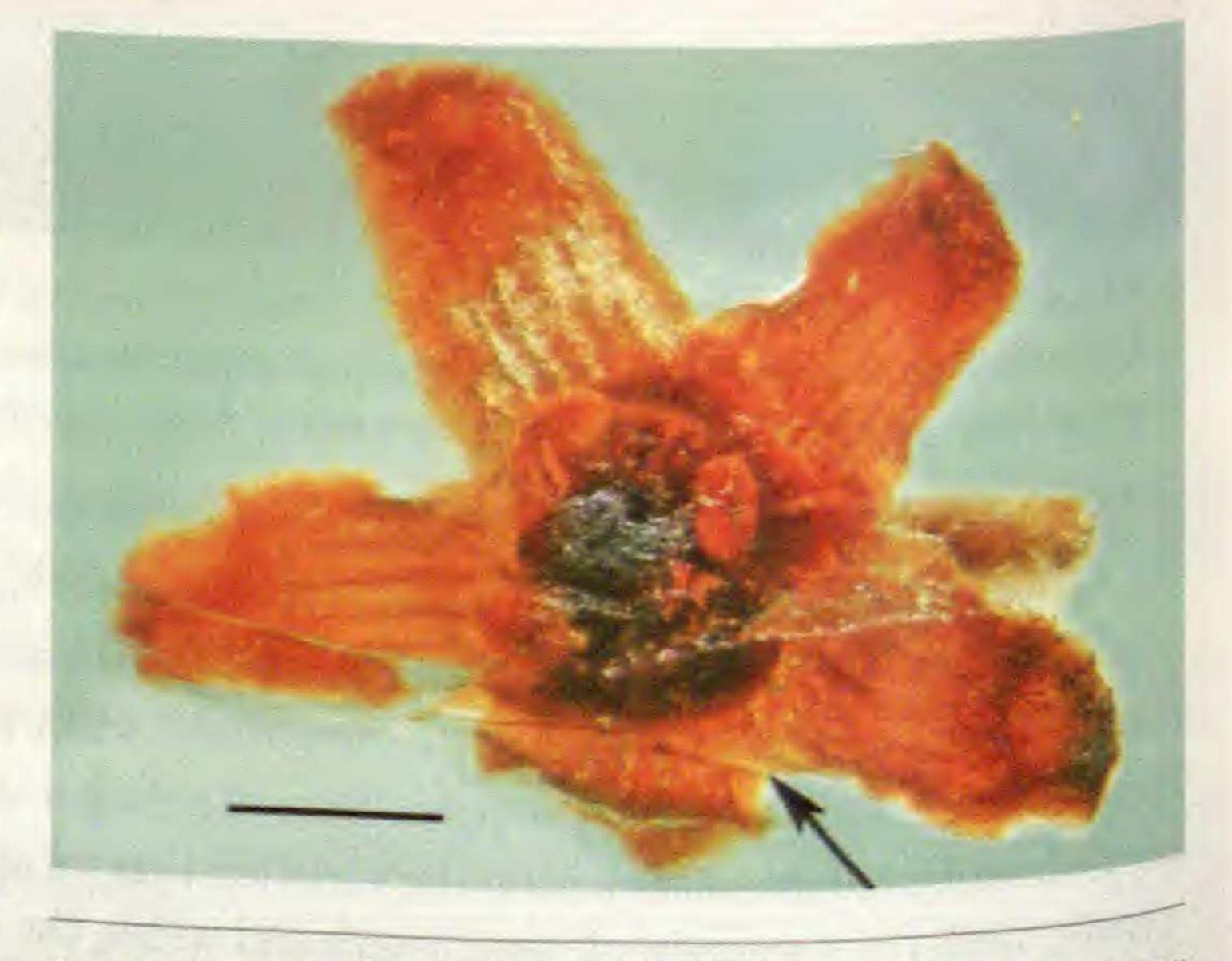


Fig. 5. Flower C, with center damaged in the process of polishing the amber. Arrow shows short region of petal overlap at the base. Bar = 0.8 mm.

ITURRALDE-VINENT, M.A. AND R.D.E. MACPHEE. 1996. Age and paleogeographic origin of Dominican amber. Science 273:1850–1852.

LAMBERT, J.B., C.Y-H. TSAI, M.C. SHAH, A.E. HURTLEY, AND J.A. SANTIAGO-BLAY. 2012. Distinguishing amber and copal classes by proton magnetic resonance spectroscopy. Archaeometry 54:332–348.

LOESENER, T. 1942. Hippocrateaceae. In: H. Harms and J. Mattfeld, eds. Die natürlichen Pflanzenfamilien. Duncker & Humblot, Berlin. Band 20b, pp. 198–231.

LONG, R.W. AND O. LAKELA. 1971. A flora of tropical Florida. University of Miami Press, Coral Gables, Florida.

MATTHEWS, M.L. AND P.K. ENDRESS. 2005. Comparative floral structure and systematics in Celastrales (Celastraceae, Parnassiaceae, Lepidobotryaceae). Bot. J. Linn. Soc. 149:129–194.

MULLER, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. 47:1-142.

POINAR, G.O., Jr. 1992. Life in amber. Stanford University Press, Stanford, CA.

Poinar, G.O., Jr. and M. Mastalerz. 2000. Taphonomy of fossilized resins: determining the biostratinomy of amber. Acta Geol. Hispanica 35:171–182.

Popov, Y.A. 1987. A new species of the bug genus *Empicoris* Wolffe from Dominican copal, with the redescription of *E. nudus* McAtee & Malloch. Stuttgarter Beitr. Naturk. Ser. B 134:1–9.

SAVOLAINEN, V., R. SPICHIGER, AND J.-F. MANEN. 1997. Polyphyletism of Celastrales deduced from a chloroplast noncoding DNA region. Molec. Phylogen. Evol. 7:145–147.

SAVOLAINEN, V., M.W. CHASE, S.B. HOOT, C.M. MORTON, D.E. SOLTIS, C. BAYER, M.F. FAY, A. DE BRUJIN, S. SULLIVAN, AND Y.-L. QIU. 2000. Phylogenetics of flowering plants based upon a combined analysis of plastid *atpB* and *rbcL* gene sequences. Syst. Biol. 49:306–362.

SCHLEE, D. 1984. Bernstein-Neuigkeiten. Stuttgarter Beitr. Naturk. Ser. C 18:1-100.

Schlee, D. 1990. Das Bernstein-Kabinett. Stuttgarter Beitr. Naturk. Ser. C 28:1-100.

SIMMONS, M.P. 2004. Celastraceae. In: K. Kubitzki, ed. The families and genera of flowering plants—dicotyledons. Springer-Verlag, Berlin. Vol. VI. Pp. 29–64.

SIMMONS, M.P., C.C. CLEVINGER, V. SAVOLEINEN, R.H. ARCHER, S. MATHEWS, AND J.J. DOYLE. 2001a. Phylogeny of the Celastraceae inferred from phytochrome B and morphology. Amer. J. Bot. 88:313–325.

SIMMONS, M.P., V. SAVOLEINEN, C.C. CLEVINGER, R.H. ARCHER, AND J.I. DAVIS. 2001b. Phylogeny of the Celastraceae inferred from 26S nrDNA, phytochrome B, atpB, rbcL, and morphology. Molec. Phylogen. Evol. 19:353–366.

SMITH, A.C. 1940. The American species of Hippocrateaceae. Brittonia 3:341-555.

Stevens, P.F. 2001 onwards. Angiosperm Phylogeny Website, Version 12, July 2012 [updated since]. http://www.mobot.org/MOBOT/research/APweb/, accessed 21 January 2013.